

ELECTRICAL ACTIVITY OF THE CORTEX ACCOMPANYING MOVEMENT

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A diversity of evidence both from laboratory experiments and clinical observation, has led to the belief that, preceding the onset of a voluntary movement, there is some activity of the large pyramidal cells (Betz cells) in the precentral gyrus. The experiments to be described were begun in an attempt to obtain direct evidence for this in healthy conscious human subjects. Previous attempts to find evidence for this activity in the electroencephalogram (e.e.g.) have failed, and the failure has been generally attributed to there being an insufficient number of neurones discharging simultaneously to produce a significantly large potential change. There were, however, two reasons which encouraged a fresh attack on the problem. First, Dawson (1947*b*), confirming and extending the observations of Grinker, Serota & Stein (1938), had found considerable potential changes over the region of the motor cortex preceding by about 15-40 msec. the onset of sudden involuntary contractions of skeletal muscle, in a patient with the diagnostic label of myoclonic epilepsy; and secondly, a technique was available which appreciably increased the sensitivity of the e.e.g. to any consistent electrical disturbance in the cortex.

METHODS

The essentials of the technique were as follows (see Fig. 1): in the typical experiment, the subject reclined in comfort, and the surface markings of the central sulcus were drawn on the scalp according to Cheine's method as described by Cunningham (1922). The electrodes were bakelite tubes about 8 mm. long and 4 mm. diameter filled with electrode jelly, into which dipped a 32 s.w.g. silver wire coated with chloride at the tip. The electrodes were firmly fixed to the scalp with collodion. In every experiment one electrode was placed 5 mm. in front of the central sulcus marking, and 7 cm. down from the midline, over a point which it was estimated would be in the region of the motor area for the hand. The position of the other electrodes was varied according to the nature of the experiment and the recording channels available. The amplifiers were of a condenser-coupled push-pull type, attenuating a 1 cyc./sec. sine wave by less than 3%, and giving a record on moving paper from a 5 cm. ink-pen which would respond without loss of amplitude to 100 cyc./sec. Two similar electrodes were applied to the skin over the flexor muscles of the forearm, and from these an electromyogram could be recorded simultaneously with the e.e.g. The subjects held a 4 cm. diameter cardboard cylinder loosely in the hand, and they were instructed to make a succession

of abrupt grips on this at a rate of about ten a minute—the instant at which a grip was made was left entirely to their own choosing. They were instructed to open or close their eyes according to the nature of the experiment.

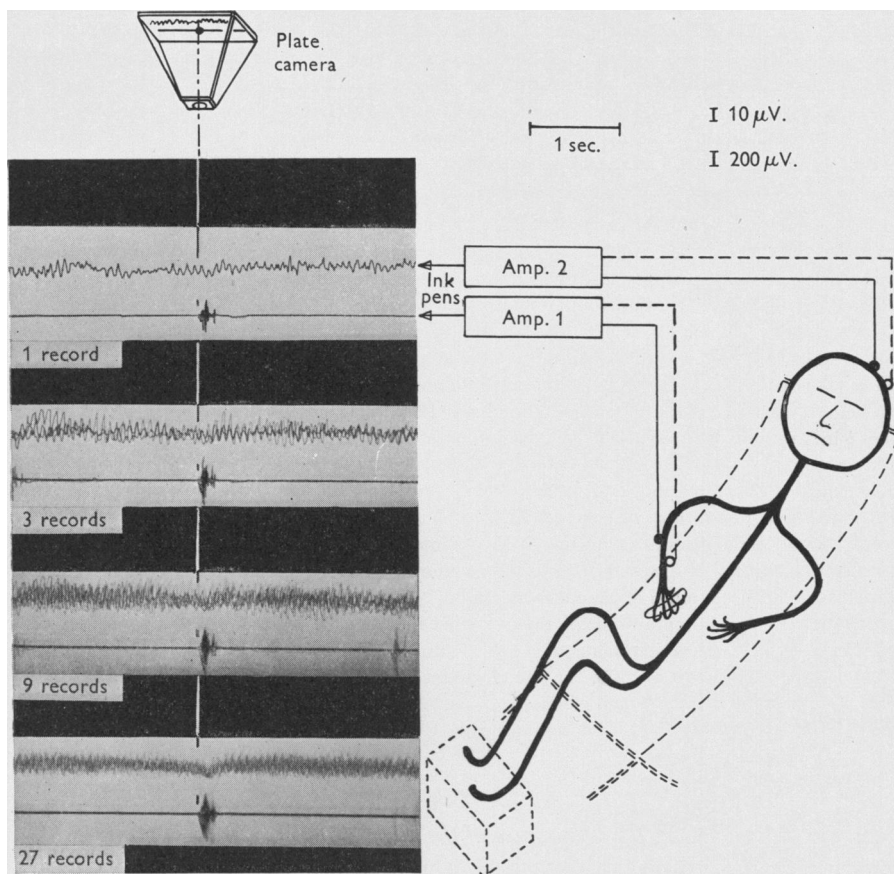


Fig. 1. Diagrammatic illustration of the experimental conditions, and the technique of photographic superimposition of the e.e.g. records with respect to the onset of muscle activity in voluntary movement as indicated by the electromyogram. In this and all subsequent figures, one electrode is shown black, and is joined to the record by a continuous line, and the other electrode is shown white and is joined by a broken line. When the white electrode goes positive with respect to the black electrode, the recording pen in that channel deflects upwards.

Inspection of a single record confirmed that no significant e.e.g. disturbance could be said to accompany the hand movement, but by the use of the following technique such disturbances were revealed. Portions of the paper record containing an electromyogram were brought in turn beneath a plate camera, and, using a celluloid graticule, they were positioned in such a way that the onset of electrical activity in the muscle group always formed an image at the same point on the plate in the camera. A brief exposure was then made—about 1/20th of the time needed to just cause complete reduction of the photographic emulsion. This process was repeated for twenty

consecutive muscular contractions, and the plate on development showed portions of the e.e.g. record superimposed with respect to the electromyogram, with the result that those changes in the e.e.g. which were consistently related in time to the electromyogram were emphasized with respect to the non-related activity. Reference to Fig. 1 shows that in the single tracing (top), it could not be said that any significant deviation in the e.e.g. had occurred. In the bottom record, however, in which the subsequent twenty-six records have been superimposed, it is clear that there has been some systematic effect in the e.e.g., and reference to the top tracing shows that this has the characteristic deviation common to the rest of the series, occurring in a burst of alpha activity.

This technique has the advantages that not only does it increase the recording sensitivity to systematic changes by an amount estimated to be about fivefold, but also it would give a chance of revealing any potential changes which might occur in the cortex before the muscle movement was made, even though the exact instant of movement was left to the subject's free choice. It has on the other hand the disadvantages that it is slow and requires careful photography to get adequate records. It must also not be forgotten that this procedure will tend to mask any consistent change in the shape of successive responses which may be occurring during the course of the series.

There is a general limitation to all attempts at accurate localization by e.e.g. recordings from the scalp surface, which arises from the variability of the positioning of the cerebral hemispheres with respect to the skull's bony landmarks. An attempt was made to estimate this variability in the case of the central sulcus on cadavers, as follows. The surface marking was drawn according to Cheine's method as described by Cunningham (1922), and small holes were drilled through the bone $\frac{1}{8}$ in. apart along the line, and the brain beneath was marked with indian ink. The skull was then opened, and the central sulcus positively identified by a coronal section. On two out of the three cadavers examined the error was, in general, greater than the width of a gyrus; in the third, it was about half the width of a gyrus. There was nothing to suggest that any correction in the method would make it more accurate. At this point the collection of further data was abandoned when it was learnt that Jasper (1949) using a somewhat better technique, had obtained a similar estimate of the unreliability of the method. In his method, a photograph of the marked scalp was superimposed on a photograph of the motor cortex identified by stimulation after reflexion of the bone flap. In view of the possibility of a variation of the order of plus or minus one gyrus, it does not appear permissible to speak of the site of the recorded activity as being more precisely located than 'in the region of the central sulcus'.

The following observations were made during the course of 120 experiments on five healthy subjects.

RESULTS

(i) *Voluntary movement and phase of the alpha rhythm.* On superimposing the records obtained in the way described, it was seen that whenever alpha activity was present, there was a tendency for the voluntary movement to occur at the same point in the phase of the cycle of the alpha rhythm on successive occasions. This is illustrated in Figs. 2 and 3, in which there is clearly a difference in the superimposed record between the centre section and the rest. It should be borne in mind that since the alpha rhythm stays roughly constant in frequency from occasion to occasion, there will be some superimposition of the waves in phase on either side of the instant of movement. This tendency was unmistakably present on some occasions in each of the five subjects—but it was not invariably present. No clear reason for this emerged, but it was characteristically more pronounced in records obtained at the beginning of an experiment than at the end. Records of the general type illustrated were obtained in about one-fifth of all the suitable data collected. The odds against

obtaining on one occasion by chance, the coincidence of twenty sine waves as good as that illustrated in Fig. 3 have been found by experiment to be about twenty to one. Since this phenomenon could be obtained on repetition, and on different subjects, there would seem to be no grounds for doubting its validity on grounds of chance.

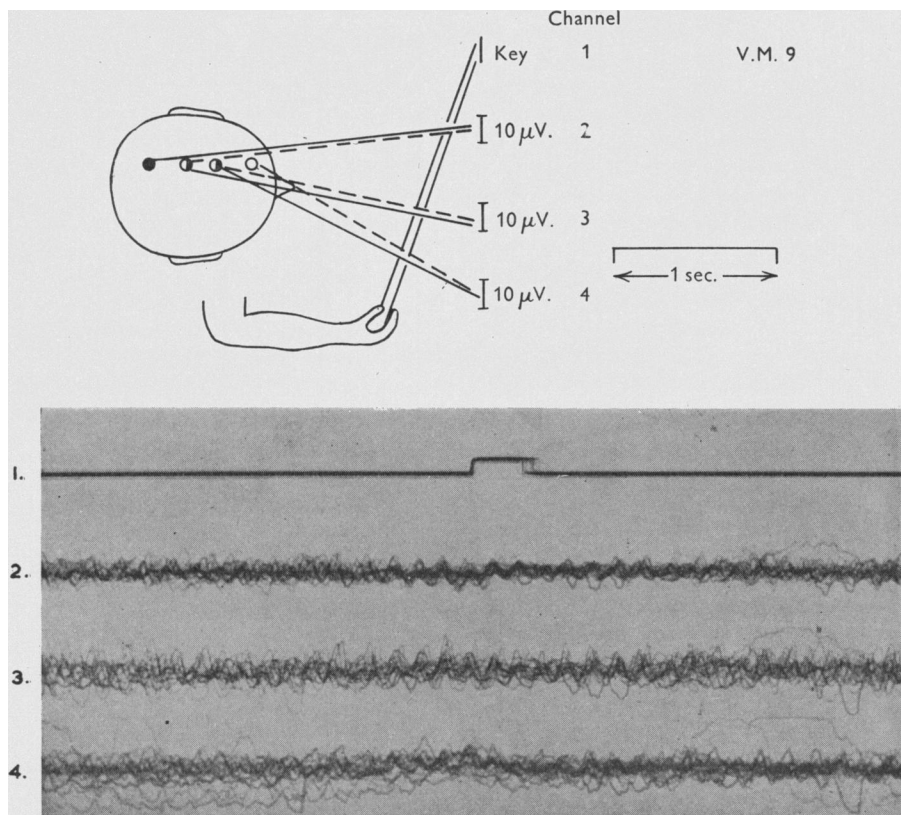


Fig. 2. Twenty tracings superimposed with respect to the instant at which a key was pressed. The alpha rhythm (channels 2 and 3) tends to be superimposed in phase for about five waves on either side of this instant. In this, and all subsequent figures, the channels are numbered from above downwards.

This tendency was not confined to voluntary hand movements, for it was also found with voluntary blinks of the eyelids. For this, the records were superimposed with respect to the blink artefact potential. Two subjects were selected for showing particularly clear alpha rhythms with their eyes open, and records of the type shown in Fig. 4 were obtained from each. It is seen that the alpha rhythms superimposed on the blink artefact, have themselves tended to be superimposed in phase. It is noteworthy that this same phenomenon has

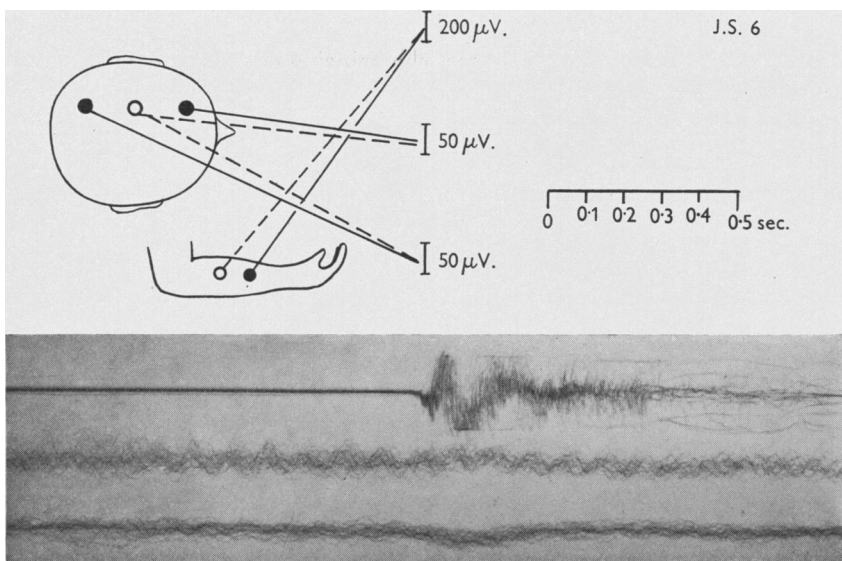


Fig. 3. The same phenomenon as shown in Fig. 2 in another subject at a faster paper speed. See also Fig. 11 in which records have been superimposed with respect to the electromyogram of a voluntary movement and of a similar movement produced by external stimulation.

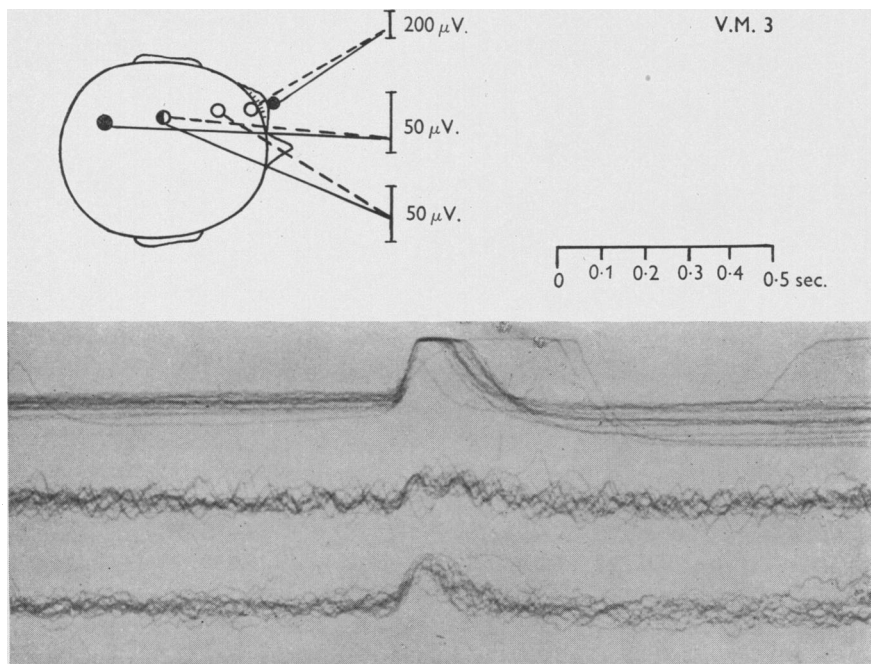


Fig. 4. Consecutive tracings superimposed with respect to an artefact caused by a voluntary blink (channel 1). The superimposed alpha waves (channel 2) are themselves superimposed on a potential wave due to the voluntary blink.

been observed quite independently by Boreham, Kibbler & Richter (1949) using an entirely different voluntary movement—in their experiments the instant of opening the eyes was found to be phasically related to the subjects' alpha rhythm.

(ii) *Potential changes accompanying hand movement.* In each subject it was found that following the hand movement, a potential change occurred in the

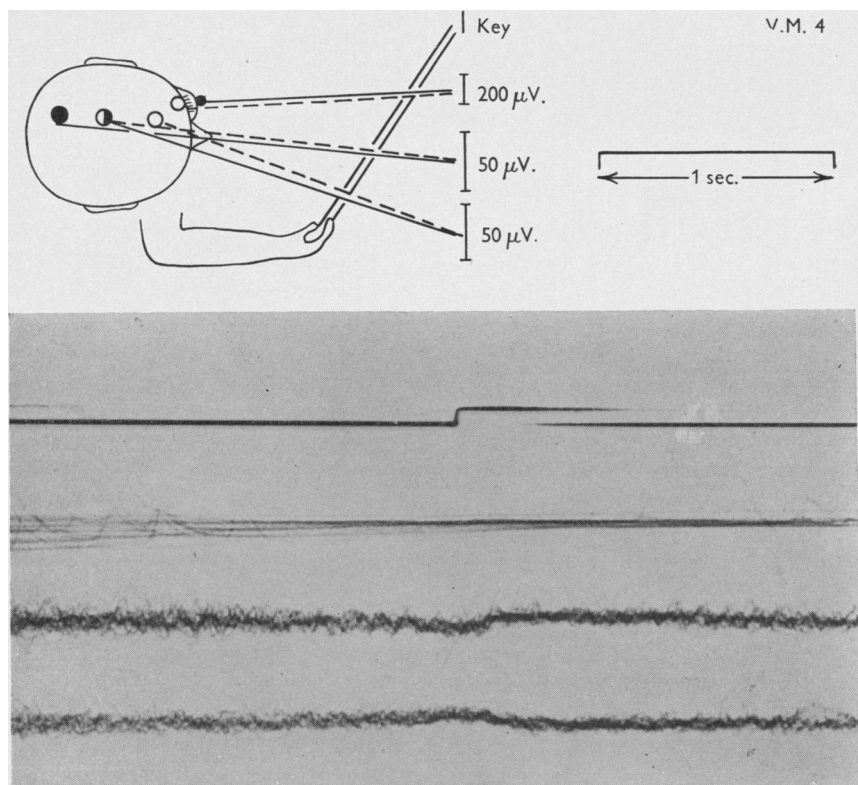


Fig. 5. Exclusion of the possibility of artefact due to concomitant blinks or eye movement. These are recorded in channel 2 and records for superimposition are selected so that there is no activity in the eye region.

e.e.g. This potential tended to be very small, particularly in the early experiments, and it appeared possible at first that it was an artefact. Instrumental artefacts, such as might be caused by swinging leads and adjacent channel interference in amplifiers were excluded by simple experiment, but the possibility that the small potentials were caused by face movements or blinking, concomitant with the hand movement, had to be tackled in more detail. For these experiments one amplifier channel was set aside to record from electrodes about the eyes and elsewhere on the face, and only those records were selected for superimposition which

showed no activity in the artefact channel. The result of this procedure is seen in Figs. 5 and 6, in which it is clear that deflexions of the base line, though in these cases small, persist in the absence of muscle activity in the eye region.

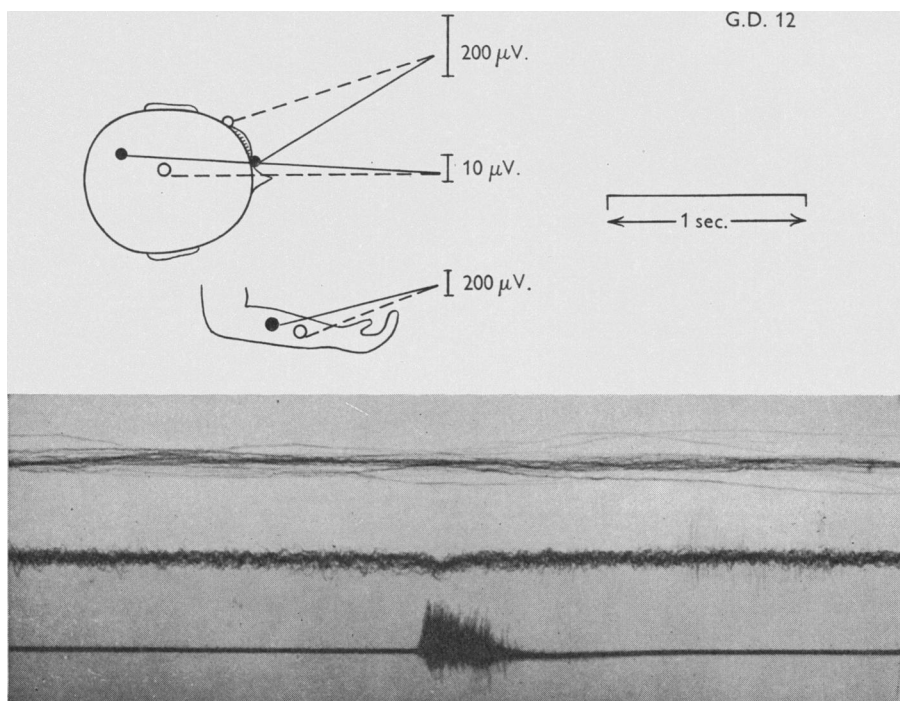


Fig. 6. A second subject showing the same phenomenon with consistent horizontal eye movements excluded (channel 1).

Two attributes of this potential change should be stressed. First, there were differences both in amplitude and form of the cortical potentials between subject and subject, and less pronounced differences between the same subject on successive occasions. The most usual response was one in which the electrode over the region of the central sulcus became negative with respect to the rest of the brain, and this effect began 20–35 msec. after the muscle activity, reaching a peak in 55–75 msec. and lasting for 100–200 msec. An unusually conspicuous response of this type is illustrated in Fig. 7, and a response of minimal significance is illustrated in Fig. 8. The response is invariably larger on the contralateral side than the ipsilateral side, and a record illustrating this is shown in Fig. 9. To obtain this, movements were made with alternate hands while the position of the head electrodes was unchanged. There is a suggestion of activity on the ipsilateral side, but there are insufficient data to indicate whether it represents a direct electrical spread or a bilateral representation. An

example of a more complex type of response is shown in Fig. 10, which will be referred to later. In responses of this type there was evidence of a positive wave succeeding the negative wave, and occasionally preceding the negative wave.

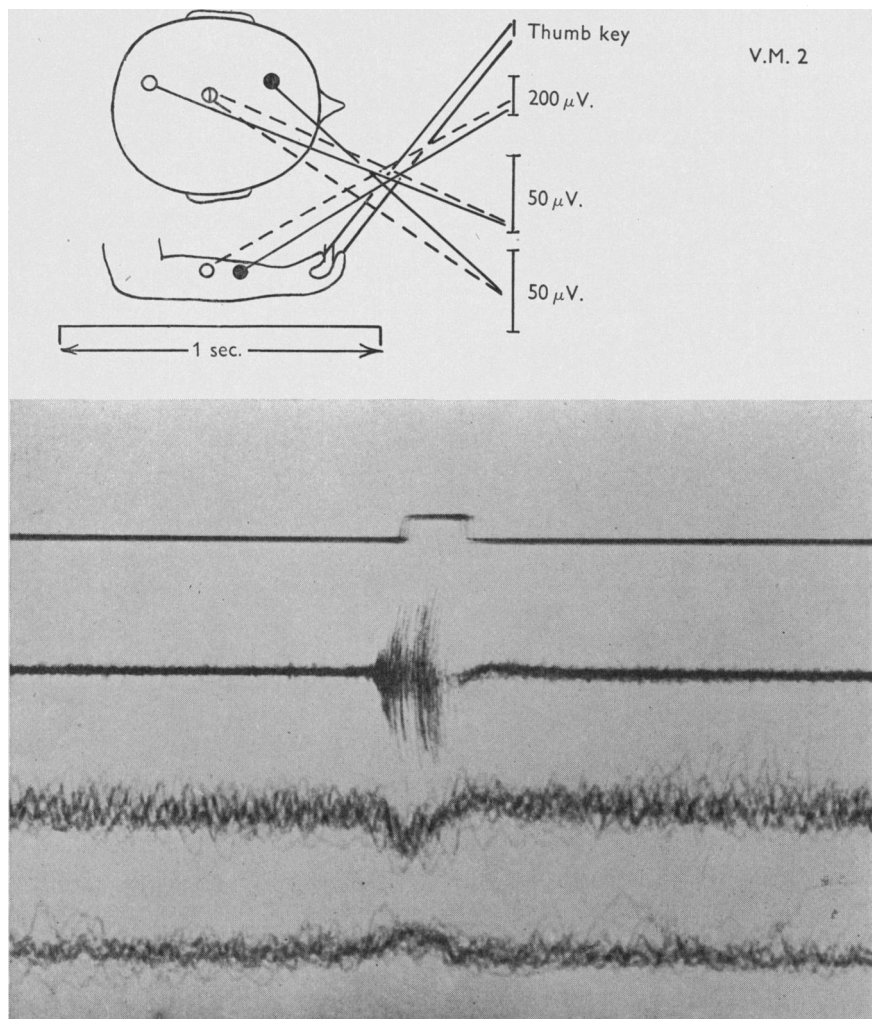


Fig. 7. Unusually large negative wave localized at the contralateral central sulcus region. Successive tracings were superimposed with respect to the onset of activity in the forearm flexor muscles, and the tracing in channel 1 gives an estimate of the errors involved in superimposing the records with respect to movement of a key. This variability is less than 15 msec. and is insufficient to mask the effect.

Classification of the types of cortical response has not been pursued in more detail. The differences are undoubtedly due to some extent to differences in the position of the electrodes relative to the active focus, but a more detailed

examination of the effect of electrode position on wave shape in one subject suggests that the predominant negative wave is relatively widespread. In view of this, it is thought that variation in localization of the electrodes from subject to subject due to anatomical differences would be unlikely to account for the whole of the difference.

Secondly, on no occasion has there been any activity recorded preceding the onset of the movement. There remained a faint possibility that a very slow potential change might be commencing before the onset of movement, and that

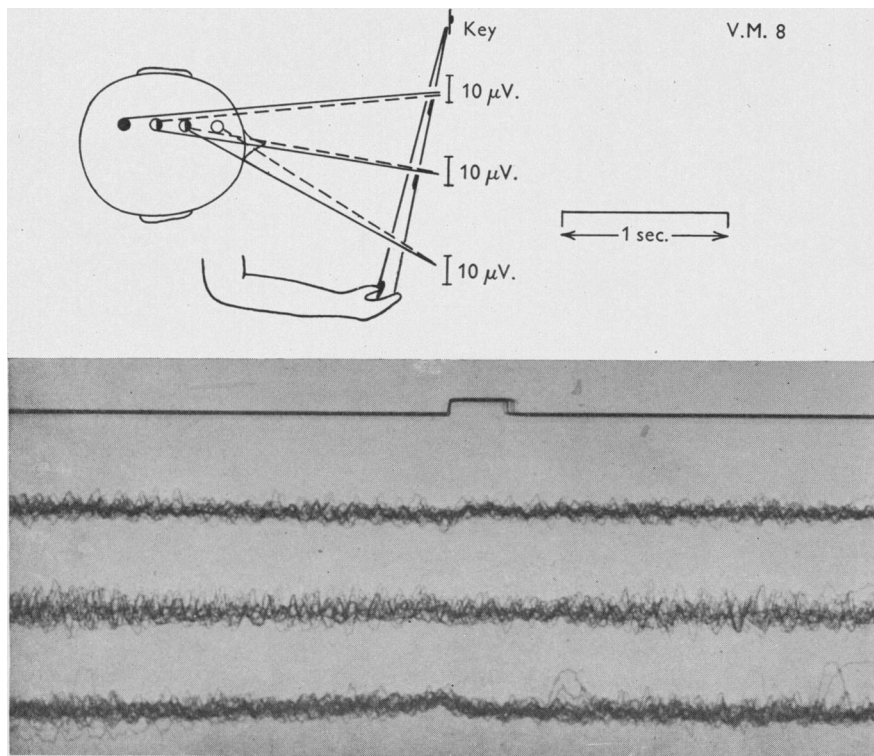


Fig. 8. Localization by the three-channel phase reversal technique. Significant but minimal changes opposed in sign in channels 2 and 4.

this slow change was being masked by the condenser coupling in the amplifiers. To examine this, one amplifier was made with an over-all time constant of 20 sec., but e.e.g. records with this did not support the idea that a slow swing in this region was being missed.

In view of the failure to find any potential changes before the onset of the movement, and in view of the duration of the delay between the onset of movement and the cortical potential changes, it was clearly necessary to determine whether the potentials could represent the arrival of afferent impulses from the

periphery. This likelihood appeared to be supported by experiments in which the basic technique was varied as follows.

A surface electrode, made of a 1 cm. diameter saline pad on a silver-silver chloride rod was strapped to the skin of the cubital fossa, and an indifferent electrode was strapped to the forearm just above the wrist. Care was taken to place the upper electrode over the median nerve in such a way that when a 20 μ sec. shock was applied between the two electrodes there was a brief 'sub-maximal' twitch of the wrist. The shock strength and electrode position were

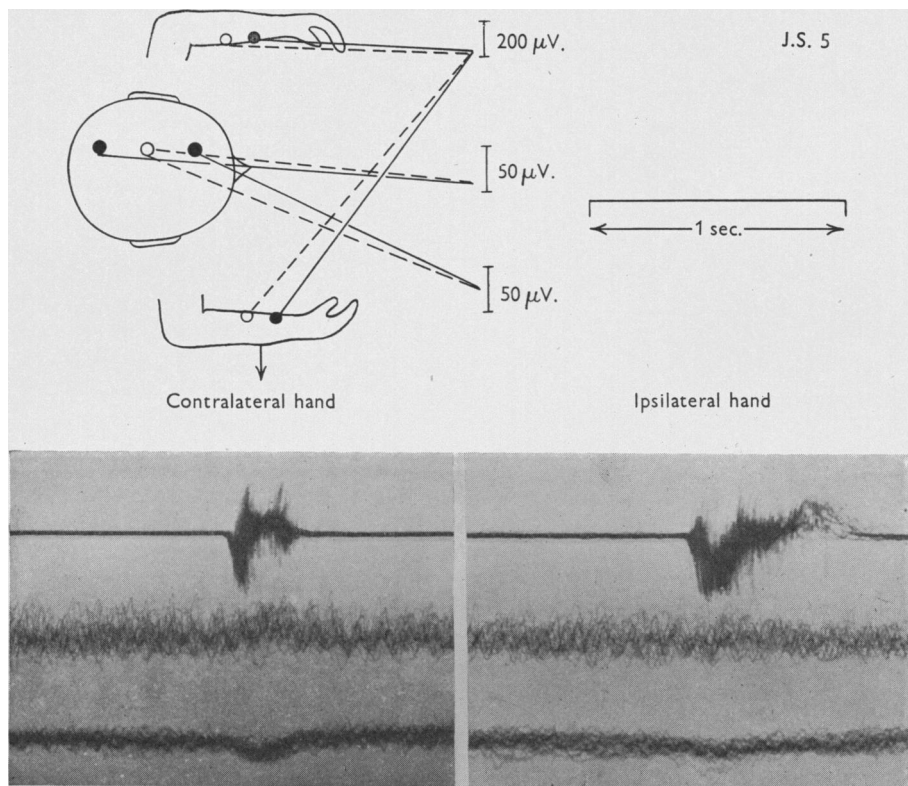


Fig. 9. Alternative experimental demonstration in another subject that the potential is larger on the contralateral side.

adjusted until there was the minimum of cutaneous sensation accompanying the shock. The experiment was conducted in the following way. The subject was asked to produce voluntarily the exact movement of the wrist that the shock produced involuntarily. It was found by close observation of the induced movement that the subject was able after a few minutes' practice to produce a voluntary movement which was identical with the involuntary movement.

An experimental run was then done, in which voluntary wrist movements alternated with involuntary movements produced by the shock. The results from an experiment of this type, which have been obtained by superimposing alternate responses, are shown in Figs. 10 and 11, obtained from different subjects. It is seen that the differences between the records from voluntary and involuntary movement are both qualitative and quantitative. In general, however, the most pronounced differences are quantitative, for the latencies of the principal components of the waves are the same in each case, and such qualitative differences as there are might be accounted for by summation of

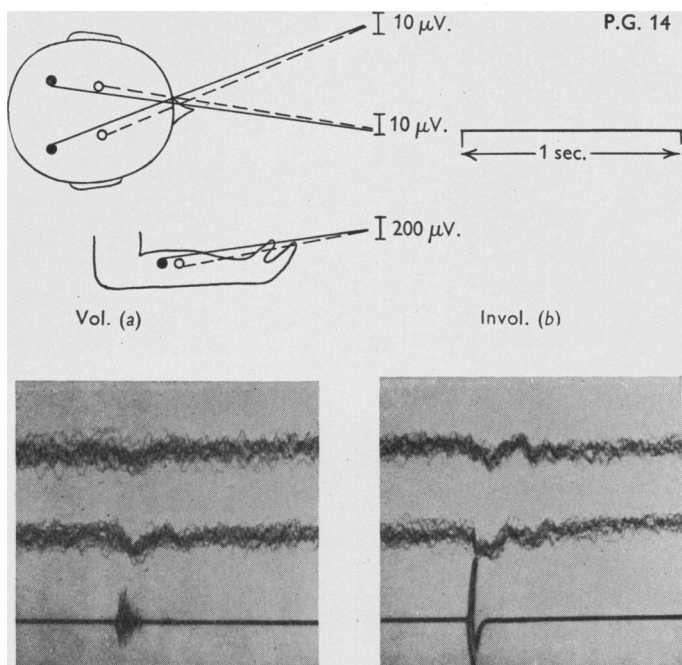


Fig. 10. Comparison between cortical responses when identical voluntary and involuntary movements of the hand are made alternately.

the original response with centripetal impulses from the stimulus itself. In Fig. 12 a well-marked cortical response similar to that illustrated in Fig. 10b is shown, when recorded on considerably faster paper. The latency of approximately 25 msec. between the stimulus and the beginning of the response is clearly seen.

Lastly, mention has already been made that this technique will mask any alteration in the shape of the response that has been occurring during the course of a single series, and may lead to an erroneous impression that the response is a wave constant in shape superimposed on random activity. In Fig. 13 the

first ten, second ten, and third ten of a series of thirty consecutive responses to involuntary hand movement have been superimposed independently, and there is a suggestion that variations in the shape of the response wave itself may be occurring.

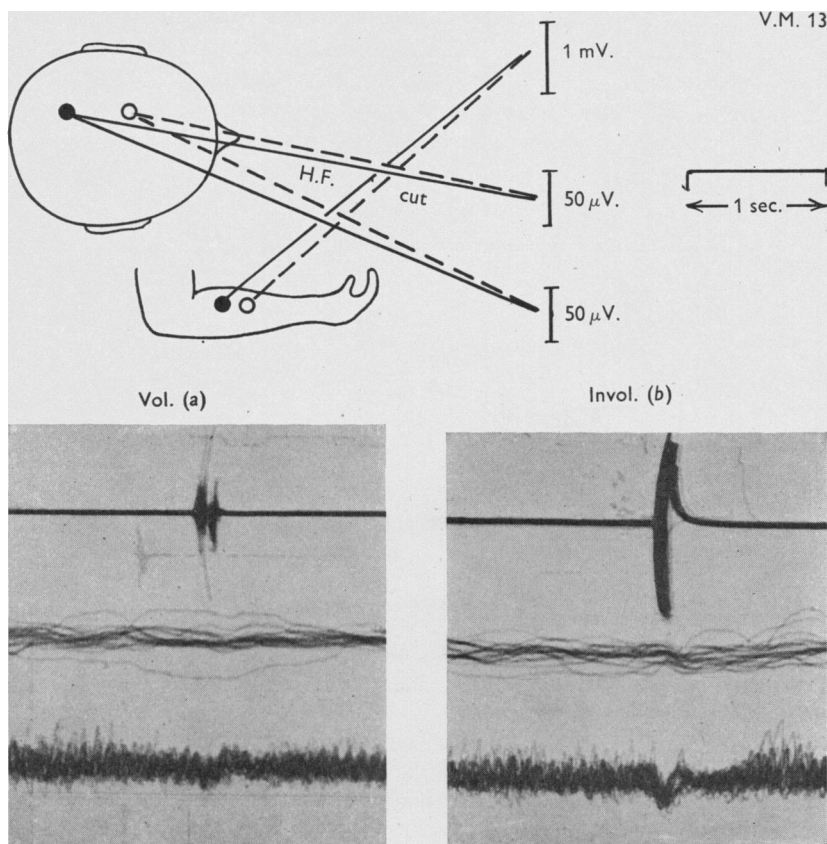


Fig. 11. The same experimental conditions as illustrated in Fig. 10 but from a different subject. The differences in response are quantitative rather than qualitative. Note that in the voluntary movement (a) there is shown the tendency for phasic superimposition of the alpha waves (see Figs. 2 and 3), which is not present when the movement was involuntary (b). The central channel had a filter to give 50% attenuation at 2 cyc./sec.

DISCUSSION

The finding that a voluntary movement tends to be timed in relation to the phase of the alpha rhythm, deserves discussion in relation to a finding by Adrian & Moruzzi (1939). They were able, in the cat anaesthetized with Dial, to record from the pyramidal tract, at its decussation in the medulla, bursts of

impulses which were synchronous with waves on the surface of the motor cortex. They further concluded that 'in so far as there is a definite rhythm in the surface potentials, we may take it as highly probable that there is a similar rhythm of discharge from the deeper cells, whatever the region concerned and whether there is an anaesthetic or not. In fact, we may conclude for example that the presence of Berger's alpha waves implies a discharge of 10 impulses a second in the axons leaving the deeper cell layers'.

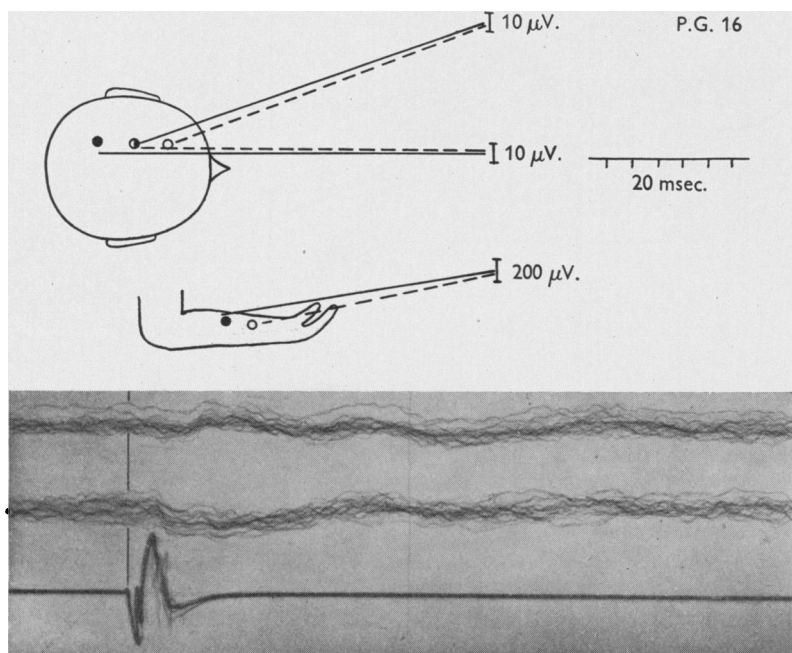


Fig. 12. Cortical response to a submaximal stimulus of the contralateral median nerve at the elbow, showing a clear latency of approximately 25 msec.

There has been much speculation concerning the function of the pyramidal tract. Broadly speaking, on the basis of clinical material, it has been identified with the existence of skilled voluntary movements, particularly of the upper extremity, and, on the basis of animal experimentation, with the existence of a normal state of tonus in the musculature. Both these viewpoints encounter difficulties. For example, in the first case, the fact that the tract is well developed in hooved mammals as shown by Lassek (1942); and in the second case, the fact that the notion largely rests on the assumption that an individual anatomical tract can alone be completely divided. On the assumption, however, that they are not entirely incorrect, these speculations taken together with the finding of Adrian & Moruzzi, might lead to the expectation that a

voluntary movement would be timed in relation to the alpha phase. For it might be supposed that pyramidal impulses coming in bursts of 10 per sec. would summate with impulses from elsewhere, with the result that there would be a maximal likelihood that those spinal centres involved in the voluntary movement would fire off in phase with the alpha rhythm. In this connexion it may be recalled that Hoffman & Stunghold (1927) have presented evidence suggesting that spinal centres subserving the stretch reflex in man fluctuate in

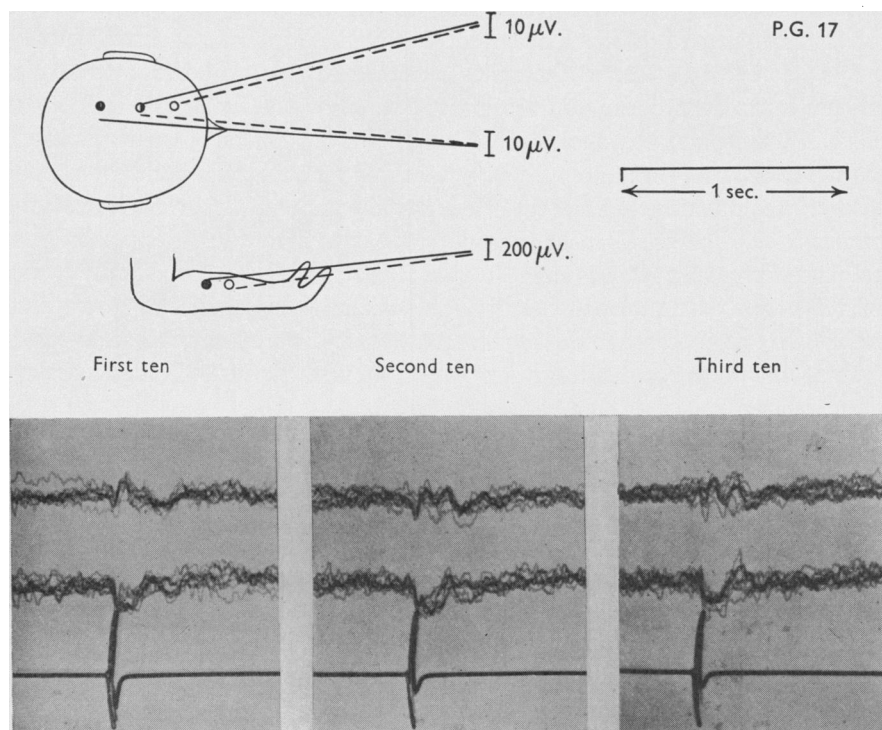


Fig. 13. Consecutive groups of ten cortical responses to median nerve stimulation to show progressive changes in the shape of the wave which would be obliterated on superimposing the thirty records.

excitability at a frequency of 10 cyc./sec. It remains to be demonstrated, however, not only that this fluctuation is correlated with the alpha rhythm, but if so, how. For it is worth noting in view of Adrian & Moruzzi's speculation, that the onset of alpha activity in the conscious human subject is not subjectively accompanied by an increase in muscle tone; if anything, the reverse. This last impression, if true, might admit the notion that the effect of these pyramidal impulses on the musculature is inhibitory rather than excitatory. There is nothing in the present data to contradict this. A tendency not to make a movement at a point in time in relation to the alpha phase might give the

same appearance in the records as a tendency to make a movement. For the present, the attempt to settle this point by indirect methods requires too many assumptions about conduction velocity to be decisive.

There are, however, some difficulties in the identification of the present finding with existing data in the ways suggested above. In the first place Jasper & Penfield (1949), reporting observations on the exposed human cortex, have failed to record 10 cyc./sec. activity when using bi-polar recording with both leads on the pre-central gyrus. They recorded instead a 25 cyc./sec. (beta) activity from these electrodes, although they could demonstrate simultaneously 10 cyc./sec. activity from electrodes placed elsewhere on the cortex. This confirms a previous finding on the intact skull reported by Jasper & Andrews (1938). If, therefore, one accepts that, under the conditions of the experiments here reported, there was no 10 cyc./sec. activity in the precentral gyrus, it is necessary to conclude that the recorded activity with which the movement was synchronized originated beneath the electrode over the parieto-occipital region; and inspection of the records suggests that this was in general so. If it happened that the beta rhythm ran at exactly double the frequency of the alpha rhythm, it might be suggested that the movement was, in fact, synchronized to a beta rhythm, but Jasper & Andrews are emphatic that the two rhythms are not simply related.

The difficulty raised by Jasper & Penfield's observation might be overcome by recalling that Lassek & Rasmussen (1939) have shown that in man not more than 3% of the pyramidal fibres arise from the large Betz cells in the motor cortex. This small proportion contains the fibres of largest diameter, but it nevertheless appears probable that a large proportion of pyramidal fibres arise from small pyramidal cells in the post-central regions—regions from which Jasper & Penfield record ample alpha activity. This, if true, might be sufficient to reconcile the present findings with the other data in the way suggested. One hesitates to accept this interpretation unreservedly however, since Adrian & Moruzzi were particular to state that 'it is only the waves from the motor area which show precise agreement with the medullary discharge'.

In discussions of the basis of skilled movement, there is one aspect which tends to be overlooked. It is that the essential attribute of skill in a movement may reside in the ability to relax a muscle group, rather than the ability to activate it. An example of a skilled movement in this category is the ability to shake down a clinical thermometer, success in which requires a relaxation of muscles acting on the wrist. This suggested that it would be interesting to determine whether the instant of voluntary relaxation of a muscle group was also timed with respect to the alpha rhythm. Some experiments were begun to examine this, but unfortunately in no case was the instant of relaxation as judged by the electromyogram sufficiently clear cut to provide a reference point for the photographic superimposition.

Finally, any complete explanation of the findings should cover the situation when movements were initiated without any reference to the alpha phase, although alpha activity was clearly present. In this connexion, it is possible that with the present method of recording a shift in the focus of the alpha activity as described by Adrian & Yamagiwa (1935) would be sufficient to account for the discrepancy if such a shift occurred during the course of one experiment. It is not obvious at the moment how to attribute biological usefulness to this mechanism, but if muscular activity is capable of potentiation 10 times per sec. by the alpha wave, it is curious that suppression of the alpha activity should occur through visual preoccupation, i.e. in environmental situations in which rapid muscular activity may be crucial.

The slow potential changes observed in the e.e.g. accompanying the hand movement are considered to represent most probably the arrival of afferent impulses at the cortex. The reason for this belief is that no potential changes are observed until at least 20 msec. after the beginning of the electromyogram (see Figs. 10 and 11) and this interval is consistent with an estimate of the peripheral delay time based on a conduction velocity of 50 m./sec. It is also noteworthy that this delay is the same in voluntary movements and in involuntary movements produced by nerve stimulation. Potential changes in the somatic receiving area of the exposed cortex have been demonstrated by Marshall, Woolsey & Bard (1941) in the anaesthetized and unanaesthetized cat and monkey, following a touch on the skin; by Marshall & Earl Walker (1949) on the unanaesthetized human cortex following a light touch on the finger. They have also been recorded by Dawson (1947 *a*) in man from the scalp when maximal stimuli were applied to either the median, ulnar, or lateral popliteal nerves. Under these various conditions the typical record showed a small and short positive disturbance, followed by a larger and more widespread negative disturbance. In the present experiments, the most conspicuous potential change over the region of the central sulcus has been a negative one. It has been preceded by a positive disturbance only when the potential has been particularly well marked, for example with the electrical stimulus on the contralateral side (Fig. 10). When account is taken of the errors in localization, and of the technical inadequacies in the e.e.g. with pen recording, and of the fact that sub-maximal stimuli were invariably used, this discrepancy is not serious.

It would be an oversimplification of the situation to picture the cortical response as some consistent wave-form superimposed on unrelated random activity. There is a suggestion that significant variations in the wave-form of the cortical response may vary from one response to the next. This was also found by Marshall *et al.* on the unanaesthetized monkey (1941, fig. 7). Dawson (1950) has also noted that when a sequence of individual cortical responses is examined, there is a tendency for particular characteristics in their outline to be grouped together rather than to be scattered irregularly throughout the

sequence. This variability may be due to summation at a cortical level, but since the cortical response is itself consequent on a thalamic relay, the summation may be occurring subcortically. Whatever the explanation, evidence that this type of variability was occurring in the present experiments is presented in Fig. 13. On this particular occasion, the subject reported that he was getting more drowsy as the experiment proceeded. This may be related, but it would require more careful control to be certain that no significant variability was present at the site of stimulation.

It is noteworthy that no disturbance of potential from this region has been recorded before the onset of muscle activity, and it is interesting that Jasper & Penfield (1949) using the more refined technique of direct cortical recording in an otherwise similar experimental situation, have also failed to find any clear change in the electrical activity of the precentral region preceding the movement. They have found instead, on hand movement, a suppression of the beta waves in a way which, they point out, is strongly reminiscent of the suppression of alpha activity on directing the attention visually. There is thus still not even suggestive evidence of localized activity in large pyramidal cells in the precentral gyrus preceding the onset of a voluntary movement. The technique now described gives an appreciable gain in sensitivity over previous methods, but if a technique is required which will detect from the scalp surface a single discharge from a single pyramidal cell, the gain in sensitivity will have to be of an entirely different order.

SUMMARY

1. The electroencephalogram (e.e.g.) has been recorded accompanying voluntary muscular movement in five healthy subjects.
2. A technique is described by which the sensitivity of the e.e.g. to systematic changes in potential is appreciably increased. This technique would also permit the recording of cortical potentials preceding a movement with which they were associated, even though the subject was left to choose the instant of movement.
3. It has been found that when alpha activity is present, there is a significant tendency for the instant of movement, as judged by the onset of activity in the electromyogram, to be related to the phase of the alpha rhythm. This finding may be consistent with others which suggest that impulses in the pyramidal tract affect the tone of skeletal muscle.
4. It has also been possible to record 20–40 msec. after the onset of the electromyogram, a small potential change in the region of the contralateral central sulcus. It is likely that this represents the arrival of afferent impulses from the periphery.
5. On no occasion has this technique revealed any potential change in the cortex preceding the onset of voluntary movement.

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